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Functionally and phylogenetically diverse plant communities key to soil biota

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Abstract. Recent studies assessing the role of biological diversity for ecosystem functioning indicate that the diversity of functional traits and the evolutionary history of species in a community, not the number of taxonomic units, ultimately drives the biodiversity–ecosystem-function relationship. Here, we simultaneously assessed the importance of plant functional trait and phylogenetic diversity as predictors of major trophic groups of soil biota (abundance and diversity), six years from the onset of a grassland biodiversity experiment. Plant functional and phylogenetic diversity were generally better predictors of soil biota than the traditionally used species or functional group richness. Functional diversity was a reliable predictor for most biota, with the exception of soil microorganisms, which were better predicted by phylogenetic diversity. These results provide empirical support for the idea that the diversity of plant functional traits and the diversity of evolutionary lineages in a community are important for maintaining higher abundances and diversity of soil communities.

Key words: above–belowground interactions; biodiversity; functional diversity; functional traits; Jena Experiment; phylogenetic diversity; plant species richness; soil fauna.

Introduction

Linking changes in community composition and diversity between trophic levels presents a major challenge for community and ecosystem ecology (Van der Putten et al. 2001, Wardle et al. 2004, Haddad et al. 2009). Particularly, understanding the links between above- and belowground communities has emerged as an important challenge given that soil biota are not just a "black box" of highly redundant species and that they drive a range of ecosystem functions (Scheu and Setälä 2002, Wardle et al. 2004). We are increasingly learning that soil biota are closely interlinked with aboveground communities and that there is a greater degree of specificity between plants and soil organisms than was previously assumed (Scheu 2001, Wardle et al. 2004,

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Bardgett and Wardle 2010). There is compelling evidence that soil biota are responsive to the quality and quantity of organic matter inputs as well as to changes in micro-environmental conditions associated with changes in plant diversity (Wardle et al. 2004, Bardgett and Wardle 2010). Despite this, a large body of literature suggests that soil biota may be less sensitive to changes in plant diversity than aboveground biota (Gastine et al. 2003, Scherber et al. 2010). However, this conclusion was mainly based on short-term studies that investigated only two facets of plant diversity, i.e., species and functional group richness (Eisenhauer et al. 2012).

Recent studies indicate that the diversity of functional traits or the evolutionary history of a community, not the number of taxonomic units, ultimately drives biodiversity–ecosystem-functioning relationships (Cadotte et al. 2009, Flynn et al. 2011). A trait is any morphological, biochemical, behavioral, and phenological characteristic of an individual that potentially affects its performance and fitness (Petchey and Gaston 2002). Identifying the most relevant functional traits underpinning the biodiversity–ecosystem-functioning relationship can be challenging, with the results sensitive to the number and choice of traits included in the analyses (Petchey and Gaston 2006). Given these potential limitations of trait-based approaches, phylogenetic diversity, the sum of the shared evolutionary history in a community, has been proposed as a useful proxy to describe the true functional diversity of a community (Cadotte et al. 2009). Phylogenetic diversity should affect ecosystem functioning if ecological dissimilarity is correlated with evolutionary divergence, meaning that the more phylogenetically divergent species are present, the more likely it is that they have dissimilar functional traits and occupy different niches, thereby differentially impacting ecosystem functioning (Felsenstein 1985, Maherali and Klironomos 2007). Additionally, plant phylogenetic diversity may be particularly important for higher trophic levels, and more than just a proxy for functional diversity if plant phylogeny reflects coevolutionary interactions between plants and other organism groups (Dinnage et al. 2012).

Lately, functional and phylogenetic diversity have been shown to be better predictors of primary productivity (Cadotte et al. 2009, Clark et al. 2012) and arthropod diversity and abundances than were plant species or functional group richness (Dinnage et al. 2012). However, we have remarkably little empirical evidence on whether these indices are superior predictors of soil biota than species and functional group richness. In addition, information on the relevance of different plant diversity indices may contribute to a better understanding of how plant diversity effects cascade into belowground food webs. Here we assess the performance of several plant functional and phylogenetic diversity metrics, alongside more conventional metrics of plant community composition such as realized plant species richness (Rdiv), functional group richness (FG) and functional group biomass as determinants of soil biota using data from one of the most comprehensive biodiversity experiments so far, the Jena Experiment (Roscher et al. 2004). We focused on the abundances and diversity of soil biota collected from 82 grassland plots with experimentally manipulated plant species (1, 2, 4, 8, 16, and 60) and functional group richness (1, 2, 3, and 4), measured on the sixth year from the onset of the diversity treatments.

Methods

Study site and experimental design.—The experimental site (50°55′ N, 11°35′ E, 130 m above sea level; mean annual temperature 9.3°C, mean annual precipitation 587 mm) was a former arable field located on the floodplain of the Saale River, Jena, Germany. The number of plant species, plant functional groups and plant identity is controlled, in a randomized four block design comprising 82 plots of 20 × 20 m. Plots were established in May 2002 with 1, 2, 4, 8, 16, or 60 perennial grassland plant species typical for local Arrhenatherum grasslands, with 16, 16, 16, 16, 14, and 4 replicates, respectively (see Roscher et al. [2004] for details on experimental design). Plant compositions in the plots were randomly chosen from a pool of 60 species and maintained by a combination of biannual mowing, weeding, and herbicide applications.

Functional diversity estimated from traits.—We selected 12 plant functional traits, based on literature-informed knowledge, that affect soil biota and processes through the quality and consistency of plant-derived organic inputs as well as through changes of microhabitat environmental conditions. For each of the 60 plant species, the traits were derived from in situ measurements (shoot biomass dry mass [mg], biomass-to-N ratio [mg N/g], shoot lignin and hemicelluloses content [%], shoot C-to-N ratio, seed mass [mg], leaf area ratio [mm^2/mg dry mass], ability to fix atmospheric N_2 [binary]) and literature surveys (seasonality of foliage [ordinal; 1, summer green; 2, partly evergreen; 3, evergreen], number of known secondary compounds, rooting type [ordinal; 1, long-living primary root system; 2, secondary fibrous roots in addition to the primary root system; 3, short-living primary root system, extensive secondary root system] and rooting depth [cm] as used by Roscher et al. [2004]; see Appendix A for details on plant traits). The traits were scaled to have a mean of zero and variance of one. The resulting trait matrix was converted into a Euclidean distance matrix and used to calculate the distance based functional diversity metrics; for calculating functional diversity (FD) the distance matrix was converted into a functional dendrogram by a UPGM clustering analysis (Petchey and Gaston 2002; see also

Appendix B). For each plant community, FD was calculated as the branch length connecting the member species of the respective community. In addition, Rao's quadratic diversity (Qr) (Rao 1982) was estimated as done by Botta-Dukát (2005) using species percentage cover (averaged for May and August 2008) to weight branch lengths between species to generate an abundance-weighted functional index that incorporates information about functional richness as well as functional evenness of a community.

Phylogenetic diversity.—A phylogeny of all 60 species in the Jena Experiment species pool was constructed based on four genes, using Bayesian methods (for details, see Allan et al. [2013] and Appendix C). Two measures of phylogenetic diversity were calculated from this phylogeny: mean pairwise distance (MPD) and mean nearest neighbor distance (MNND). MPD measures the mean phylogenetic distance between all pairs of species (close and distant relatives) and is affected by the number of deeper splits in the phylogeny. MNND measures the mean distance between each species and its closest relative and therefore measures diversity only at the tips of the phylogeny. However, several communities had high MPD but low MNND, providing the justification for including both measures in our analyses.

Soil organism and plant sampling.—Five soil cores (5 cm diameter, 5 cm depth) were taken from each plot for determining microbial biomass (Cmic). The pooled five samples were homogenized, sieved (2 mm) to remove larger roots, animals, and Cmic was measured using an O_2-microcompensation apparatus (Scheu 1992). Glucose was added to saturate the catabolic enzymes of the microorganisms (4 mg/g dry mass added as solution to increase the water content to the water holding capacity of the soil). The mean of the lowest three hourly readings within the first 10 h was taken as maximum initial respiratory response (MIRR; $\mu L\ O_2 \cdot h^{-1} \cdot g$ soil dry $mass^{-1}$) and microbial biomass (μg C/g soil dry mass) was calculated as 38 × MIRR (Beck et al. 1997). Belowground macro- and mesofauna were Tullgren extracted from one large (20 cm diameter, 20 cm depth) and one small (5 cm diameter, 10 cm depth) soil cores per plot. Diversity of arbuscular mycorrhizal fungi (AMF) was analyzed using a molecular TaqMan qRT-PCR assay designed after initial ITS PCR based inventory of the AMF species list present at the site (Konig et al. 2010). Plant species cover was estimated from a 9-m^2 subplot in each plot, whereas the aboveground plant community biomass was the average of the late May and late August (year 2008) harvests by clipping the vegetation at 3 cm above ground in four rectangles of 0.2 × 0.5 m per plot (see Weigelt [2010] for methodological details on measurements of plant biomass and cover estimates). Data on soil biota have been used previously to explore the effects of plant species and functional groups (Eisenhauer et al. 2010, Scherber et al. 2010), but have not been used to test functional or phylogenetic diversity indices.

Statistical analyses.—We used path analysis, a particular case of structural equation modeling involving only measured variables, to test the support for multiple potential drivers while accounting for the unavoidable colinearities among the explanatory variables (Grace 2006; see also Appendix D). As the calculation of the abundance weighted functional and phylogenetic diversity indices was based on the realized species richness (Rdiv) from the same year as the soil biota samplings (year 2008), we therefore preferred to use the year 2008 Rdiv in the analyses (note that Rdiv is highly correlated with sown species richness [Pearson's r (realized, sown) = 0.99]). For each response variable (see Appendix E) a full model of causal relationships was created including simultaneously several hypothetical pathways through which log-transformed (to reduce leverage and linearize relationships) Rdiv could affect soil biota. The full model (see Appendix F) included a direct pathway between Rdiv and soil biota abundance/diversity and several indirect pathways via functional diversity indices (FD and Qr), phylogenetic diversity indices (MPD and MNND), functional group richness (FG) and functional group biomass (i.e., the biomass of legumes, grasses, small herbs, and tall herbs). We included the path between Rdiv and the other diversity measures because the Jena Experiment manipulated species richness and therefore variation in functional/phylogenetic diversity is caused by variation in species richness and composition between plots. Functional and phylogenetic diversity were in turn hypothesized to affect soil biota directly or indirectly via several measures of plant biomass (shoot, root, and total) as plant productivity has been shown to be an important driver of belowground communities (Spehn et al. 2000). A continuous variable (percent clay content in the upper 10 cm soil layer ranging from 13.7% to 25.6% was preferred to the block variable to account for the variability in soil texture. The full models were simplified by step-wise exclusion of variables with nonsignificant regression weights and nonsignificant covariances as estimated by AIC (Akaike information criterion) scores until a minimal adequate model was achieved. Minimal adequate models were indicated by non-significant differences when comparing the predicted and observed covariance matrices (χ^2 tests with $P > 0.05$), by lower AIC, lower root mean squared error approximation (RMSEA <0.05) and higher comparative fit index (CFI > 0.90) (Grace 2006, Arbuckle 2009). Path analysis was performed using the SPPS Amos 18 statistical package (Arbuckle 2009). Scatter plots with univariate linear regression line were produced in R 2.15.0 (R Development Core Team 2012) for visualizing the direction of the relationship between the soil biota and the different diversity indices (Appendix G). Data on abundance and diversity of the soil biota was square-root transformed to

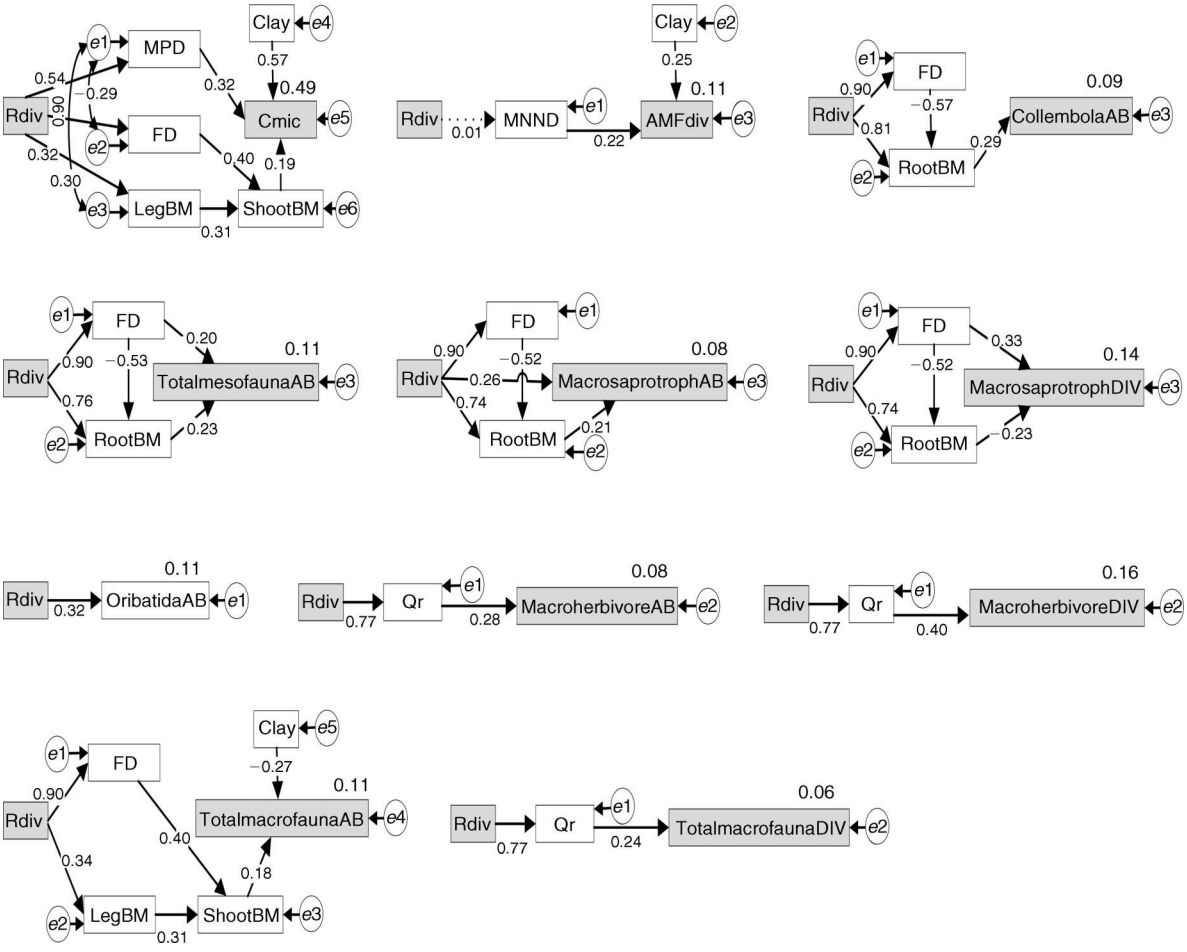

FIG. 1. Minimal adequate models for the effects of multiple plant community predictors on the abundance and diversity of various groups of belowground organisms (see Appendix F for the maximal model). Solid arrows show significant relationships (pathways) between variables, dotted arrows indicate a nonsignificant relationship, and numbers next to arrows show standardized parameter estimates (i.e., standardized regression weights). Circles (e1–e6) indicate error terms, and double-headed arrows indicate significant correlations between the error terms. Squared multiple correlations (R^2) for the predicted/dependent group of soil biota is given on the box of the dependent variable. Abbreviations are: Rdiv, realized plant species richness; Cmic, microbial biomass; AMFdiv, arbuscular mycorrhizal fungal diversity; CollembolaAB, abundance of Collembola; OrbatidaAB, abundance of Oribatida; TotalmesofaunaAB, total mesofauna invertebrate abundance; MacrosaprotrophAB, macrofauna decomposer invertebrate abundance; MacrosaprotrophDIV, macrofauna decomposer invertebrate species richness; MacroherbivoreAB, macrofauna herbivore invertebrate; MacroherbivoreDIV, macrofauna herbivore invertebrate species richness; TotalmacrofaunaAB, total macrofauna abundance; TotalmacrofaunaDIV, total macrofauna species richness; FD, functional diversity; Qr, Rao's quadratic diversity; MPD, mean pairwise phylogenetic distance; MNND, mean nearest neighbor phylogenetic distance; LegBM, biomass of legumes; RootBM, root biomass; ShootBM, shoot biomass. No adequate models with significant regression weights could be obtained for abundance of Gamasida, abundance of Symphyla, macrofauna predator abundance, and macrofauna predator species richness (see Appendices H and I for full results of the path analysis).

reduce heteroscedasticity of error variances, whereas microbial biomass was log-transformed to improve normality. Although variables such as total mesofauna and macrofauna abundances and diversity are not independent from the comprising subordinate groups, we consider them informative because independent data sets with abundances and diversity of multiple trophic levels of soil biota as well as in-situ collected plant functional traits are rarely available. In addition, it is unknown whether diversity and abundance of these groups respond similarly to functional and phylogenetic plant diversity.

RESULTS

Plant functional or phylogenetic diversity indices were retained as significant predictors of soil biota diversity and abundance in 10 out of the 11 minimal adequate path analysis models, while direct effects of realized species richness (Rdiv) were retained in just two models (Fig. 1, Appendixes H and I). Rdiv is correlated with

most of the other diversity measures (Appendix D), therefore the path between Rdiv and the other diversity measures was retained in almost all models; however the lack of direct paths between Rdiv and soil biota diversity and abundance indicates that Rdiv is a less important predictor for soil biota than functional/phylogenetic diversity. No minimal adequate models could be achieved for the abundances of gamasid mites and Symphyla or for the diversity and abundance of macropredators. Rao's quadratic diversity (Qr) was retained as the sole predictor in the models predicting the abundance and diversity of herbivores (Fig. 1) and the diversity of macrofauna. Functional diversity (FD) was retained in six of the eleven adequate models and affected soil biota directly but also indirectly (via plant shoot or root biomass). Note that direct paths indicate effect pathways unrelated to plant biomass. Plant shoot biomass was retained as a significant predictor in the models for microbial biomass and the total abundance of macrofauna (Fig. 1), which was in turn affected by the amount of legume biomass and FD. Root biomass was retained in the models for predicting the abundance of Collembola, mesofauna and macrosaprotrophs and the diversity of macrosaprotrophs. Phylogenetic diversity was retained in the models predicting microbial biomass (retained MPD) and the diversity of arbuscular mycorrhizae (retained MNND). In all minimal adequate models, the standardized and unstandardized regression weights (Fig. 1, Appendixes H and I) indicate that higher functional or phylogenetic diversity led to higher abundances and diversity of the analyzed taxonomic groups (Appendix G) and increased plant root and shoot biomass.

Discussion

Functional and phylogenetic diversity indices have been proposed as a pragmatic and more accurate way of capturing potential niche complementarity in a community (Cadotte et al. 2009, Clark et al. 2012). While it often has been shown that plant functional and phylogenetic diversity drives aboveground communities and processes (Cadotte et al. 2009, 2012, Flynn et al. 2011), little empirical evidence is available showing that it is also a key determinant of soil communities. The findings of this study provide strong evidence that belowground communities increase in complexity (abundances and species richness) in response to increased plant functional diversity. The results also show that functional and phylogenetic diversity metrics outweigh the traditionally used species and functional group richness as predictors of soil taxa abundance and diversity. Measuring multiple functional traits should provide a higher resolution picture of potential niche complementarity in a community beyond what species or functional group richness can explain since not every species increases functional diversity by an identical amount (Petchey and Gaston 2002). Furthermore, additional mechanisms emerging from niche complementarity such as increased microhabitat heterogeneity (Eisenhauer et al. 2011), substrate diversity (Spehn et al. 2000), and asynchronous population fluctuations (Roscher et al. 2011), all of which have been shown to contribute to increased ecosystem stability (Naeem and Li 1997, Milcu et al. 2010), can be better captured by functional diversity (Flynn et al. 2011, Cadotte et al. 2012). This is in contrast to previous studies showing that soil organisms mainly respond to the presence of certain plant functional groups (e.g., N_2 fixers [Spehn et al. 2000, Milcu et al. 2008]) and underlines the importance of considering multiple plant traits in functional metrics aiming to predict belowground communities.

Recent studies have emphasized the importance of the diversity of plant evolutionary lineages for ecosystem functioning and diversity of arthropods (Cadotte et al. 2012, Dinnage et al. 2012), and here we show that the evolutionary history of the plant community (measured as phylogenetic diversity) also drives mycorrhizal diversity and soil microbial biomass. This supports the existence of strong coevolutionary links between soil microorganisms and plants and the existence of specific associations between plants and microorganisms (Reynolds et al. 2003, Eisenhauer et al. 2010). Arbuscular mycorrhizae are obligate biotroph symbionts that form tight associations with their host plants, and recent studies using network theory to link the diversity of host plants and of arbuscular mycorrhizae found a nested relationship pattern suggesting strong specialization (Montesinos-Navarro et al. 2012). As these groups are important for plant nutrient uptake and decomposition, and a high mycorrhizal diversity has been shown to be associated with higher plant biomass production (Maherali and Klironomos 2007), their greater abundance in phylogenetically diverse communities might also partially explain the increase in plant biomass with plant phylogenetic diversity (Cadotte et al. 2009).

In our study, FD and Qr were superior predictors of soil biota for meso- and macrofauna, which suggests that these groups instead respond to the diversity in traits affecting plant resource quality and micro-environmental changes. This suggests that different soil organisms are specialized on different types of plant resources and plant communities with higher diversity of resources support more abundant and diverse meso- and macrofauna.

Plant traits are not stable plant characteristics, but vary with growing seasons, environmental (Ackerly and Cornwell 2007) and diversity gradients (Gubsch et al. 2011), or even at a given time point within populations (Albert et al. 2010, Clark 2010). In spite of efforts to incorporate intraspecific trait variation in measures of functional diversity (Albert et al. 2010) and the relative amount of variation in different traits (Clark et al. 2012), it

is unclear how this variation could best be included in modeling relationships between functional trait diversity and processes related to other trophic levels, which also are not constant temporally. It is usually assumed in trait-based approaches that within-species trait variation is smaller than between-species trait variation (McGill et al. 2006). Nevertheless, we cannot exclude the possibility that missing or weak relationships between plant functional diversity and soil biota were due to not incorporating intraspecific trait variation. However, the many significant effects of functional trait diversity that we did find suggest that the majority of belowground organism groups respond to interspecific variation in functional traits.

Predator trophic levels (gamasid mites and macro-predators), did not respond to any of our measures of plant diversity. This is in line with previous studies indicating that effects of species diversity of one trophic level become weaker with the trophic distance (De Deyn et al. 2004, Scherber et al. 2010). Moreover, it suggests that the failure to detect bottom-up effects of plant species richness on predatory trophic levels is not simply due to overlooking indirect effects via functional and phylogenetic diversity. Instead, top-down (Haddad et al. 2009) or environmental drivers probably shaped the abundance and diversity of predatory communities.

The multiple pathways through which species richness can affect the diversity and abundance of soil fauna emphasizes the multidimensionality of factors involved in plant–soil interactions. While many of the plant functional and phylogenetic effects where direct, in some cases they were mediated by plant productivity, e.g., soil microbial biomass increased with shoot biomass (which in turn was affected by the presence of legumes and functional diversity), but also with phylogenetic diversity. Shoot biomass has previously been suggested to affect microbial biomass through the amount of root exudates entering the soil (Eisenhauer et al. 2010). Furthermore, root biomass was also retained in several models as an indirect pathway through which functional diversity affected abundances and diversity of saprotrophic fauna, in line with previous studies underlining the role of the quantity of belowground inputs for decomposer food webs (Pollierer et al. 2007, Bardgett and Wardle 2010).

Overall, the relationship between functional diversity and belowground communities may still seem somewhat weaker when compared with aboveground food webs (Scherber et al. 2010). However, it is highly unlikely that there will ever be a "perfect" index of functional diversity able to equally predict the response of all trophic levels (Petchey and Gaston 2006). Moreover, the heterogeneous nature of the soil environment at different spatial and temporal scales poses a major challenge for ecologists trying to quantify the importance of biotic determinants of soil communities and very likely explains the low effect sizes detected in some studies so far (Gastine et al. 2003, Viketoft et al. 2009). Despite some limitation of the used metrics (e.g., unknown effects of plant functional trait variation), the results provide strong evidence that soil biota are responsive to facets of plant diversity such as functional and phylogenetic diversity and add to the mounting evidence that plant diversity is a key driver of belowground communities and ecosystem functioning (Zak et al. 2003, Milcu et al. 2008, Eisenhauer et al. 2012).

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Supplemental Material

Appendix A

A table with the means and standard deviations of the 12 functional traits derived from the 60 species present in the Jena Experiment (*Ecological Archives* E094-170-A1).

Appendix B

Dendrogram representing the relationships between the 60 species present in the Jena Experiment based on functional traits (*Ecological Archives* E094-170-A2).

Appendix C

Maximum clade-credibility phylogeny of the 60 species in the Jena Experiment (*Ecological Archives* E094-170-A3).

Appendix D

Correlation matrixes of predictors (*Ecological Archives* E094-170-A4).

Appendix E

A table presenting the different groups of soil biota sampled in year 2008 (*Ecological Archives* E094-170-A5).

Appendix F

A schematic of the maximal model used in structural equation modeling (*Ecological Archives* E094-170-A6).

Appendix G

Scatter plots with linear regression line for visualizing the direction of the relationship between the soil biota and the different diversity indices (*Ecological Archives* E094-170-A7).

Appendix H

Model fit estimates for the minimal adequate models (*Ecological Archives* E094-170-A8).

Appendix I

Standardized and unstandardized maximum-likelihood estimates for the minimal adequate structural equation models (*Ecological Archives* E094-170-A9).